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TIGER BEETLES OF THE GENUS *CICINDELA* IN THE SULPHUR SPRINGS VALLEY, ARIZONA, WITH DESCRIPTIONS OF THREE NEW SUBSPECIES (CICINDELIDAE — COLEOPTERA)

by

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ABSTRACT: The Sulphur Springs Valley of southeastern Arizona contains a large tiger beetle fauna. Seventeen species of *Cicindela* (Cicindelidae - Coleoptera) are reported; of these, three are described as new subspecies: *C. willistoni sulfontis*, *C. pulchra dorothea* and *C. nevadica citata*. Ecological associations of each species are detailed and a key is provided for identification. The relationships with other subspecies are mentioned, with special emphasis on the three subspecies described. The *Cicindela* fauna of the valley is shown to be related, for the most part, to the fauna of the mid-Rio Grande River System, indicating that past physical geology of the lower Southwest allowed hydrographic flow in an eastward direction, at least as early as the Miocene. In late Pliocene or early Pleistocene, stream flow began going in a westerly direction allowing some migration of species in that direction. This had a limited effect on the tiger beetles of the Sulphur Springs Valley because this valley remained isolated during most of the Pleistocene.

INTRODUCTION

Many of the western United States tiger beetles of the genus *Cicindela* have undergone subspeciation. This is particularly evident in the Southwest where profound geological changes have occurred, especially during late Cenozoic. These changes have produced environmental dislocations and have altered climate in such diverse ways as to induce strong ecological pressures on the various populations. The Sulphur Springs Valley of southeastern Arizona has been totally isolated geologically from adjacent valleys at least through the latter part of the Pleistocene when it became an area of internal drainage. The *Cicindela* fauna of this valley contains a large number of species, some of which have uniquely subspeciated. The subspecies described in this paper are isolated from the main populations of their respective species, some by a considerable distance, thus extending our knowledge of the geographical limits of these species. Students and collectors of tiger beetles have been attracted to this valley for the past twenty years be-

cause of its rich fauna. During this same period the author has conducted fifteen field trips into the valley, and has accumulated over two thousand specimens for this study.

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PHYSIOGRAPHY OF THE SULPHUR SPRINGS VALLEY

The Sulphur Springs Valley lies in the mountainous region of Arizona, south of the plateau region, and east of the desert region. The mountains are of the block-fault type, similar to those of the Basin and Range province of Utah and Nevada, but appear to be older. The valley lies across the center of Cochise County and extends northward into the southern portion of Graham County; it trends in a north-northwestward direction from the Mexican border for about 145 kilometers, with an average width of about 32 kilometers. The valley covers about 4700 square kilometers and drains another 2600 square kilometers of the bordering watershed. The 32nd parallel crosses the valley just south of the large central playa, while the 110th meridian traverses to the west of the playa. The valley is bounded on both sides by mountain ranges which separate it on the east from the San Simon Valley, and on the west from the San Pedro Valley; both of these valleys drain northward into the Gila River basin. The Sulphur Springs Valley is separated on the southeast from the San Bernardino Valley by the Perilla Mountains, however, this smaller valley and the southern third of the Sulphur Springs Valley drain to the south into the Yaqui River system of Sonora, Mexico.

The mountains that enclose the valley from the east include the Pinalino, Dos Cabezas, Chiricahua, Pedregosa, and Perilla mountains. The western chain includes the Galiuro, Winchester, Little Dragoon, Dragoon, and Mule mountains. The mean elevation of the valley is slightly over 1300 meters. The climate is semi-arid as the central portion receives an average yearly rainfall of less than 30 centimeters. There is a rainy season which begins in mid-July and lasts through September.

The center of the valley contains a large, roughly triangular playa that covers about 132 square kilometers and drains the upper two thirds of the valley. This playa lies a few kilometers south of the town of Willcox, at an elevation of 1257 meters. During pluvial times this basin of internal drainage contained a lake that was approximately 32 kilometers long by 18 kilometers wide, thus covering an area of about 311 square kilometers to a depth of 13.5 meters. This Pleistocene lake was named Lake Cochise by O. E. Meinzer (1913:34), and then as now, had no outlet. An extensive wind-built sand and clay region lies south and west of Willcox. This region is characterized by scattered ridges and hills, some as high as 15 meters and several kilometers long, laid out in no specific pattern, but separated from each other by ponds or depressions which fill with water during the rainy season and are capable of holding this water for a considerable time thereafter.

The isolation of the Sulphur Springs Valley, its unique drainage system which is partially south but mostly internal, the peculiarities of the topography where water can remain in blowouts for extended time are factors which contribute to the valley's ability to sustain a large diversified tiger bettle fauna.

SYSTEMATIC ACCOUNT

Genus **Cicindela**

Cicindela willistoni sulfontis Rumpp, new subspecies.
(Figure 1a.)

DESCRIPTION.—Medium in size, narrow, convex, robust in form; color dark blue-green, green-

ish bronze, or brown; dull above, brilliant below; maculation broad, connected along edge of elytra HEAD: A few white hairs on vertex just above frons in interocular space. ELYTRA: The maculation consists of a broad C-shaped humeral lunule. The middle band is extended upward along the edge of the elytra to meet the humeral lunule, also considerably downward to join the apical lunule; the band enters the edge with only a slightly downward direction, then bends suddenly so that it is nearly parallel to the suture for a long distance before it ends in an inwardly directed bulb; the apical lunule is broad at the tip with its inner edge extending outwardly and down toward the edge where the lunule bulges without recurving. DIMENSIONS: Holotype male, green - length 13.0 mm, width 4.8 mm. Allotype female, brown, similar to the male but broader - length 13.0 mm, width 5.4 mm.

ETYMOLOGY.—This subspecies is named for the Sulphur Springs Valley by combining the Latin *sulfo* (sulphur) with *fontis* (a spring).

THE TYPE SERIES.—Until 1965 the type series consisted of only 4 specimens collected between 5 and 9 kilometers southeast of Willcox, in a region of wind carved sinks. In August of 1969 Mr. Jay M. Sheppard discovered the primary habitat at which time large series were obtained. The type location is 5.6 kilometers west-southwest of Willcox, on the playa, and a few hundred meters south of the tracks of the Southern Pacific Railroad. All paratypes from the north shore of the playa, as all those from the blowouts to the east are considered paratypical topotypes; all specimens are assumed to be from the same general population.

The type series consists of 217 specimens distributed as follows: Holotype, male, type no. 12,530 in the collection of the California Academy of Sciences; allotype, female, in the N. L. Rumpp Collection (NLRC). There are 215 paratopotypes of which 68 are in the NLRC, 86 in the collection of Rev. Bernard Rotger, C.R., of Pagosa Springs, Colorado, 53 in the collection of Jay M. Sheppard of Laurel, Maryland, and 2 each in the collections of the American Museum of Natural History (AMNH), New York City, the U.S. National Museum (USNM), Washington, D.C., and the California Academy of Sciences (CAS), San Francisco, California.

VARIABILITY.—The elytral maculation is strikingly constant, but the color is either green or brown with few intermediates. This is shown in Table 1.

TABLE 1. Distribution of color and sexes in the type series of *C. willistoni sullontis*.

Collector	Date	green		brown		intermediate	
		male	female	male	female	male	female
F. H. Parker	13:X:1949		1				
N. L. Rumpp	2:X:1961	1	1				
N. L. Rumpp	13:X:1964		1				
G. Gaumer	VII:1969						1
J. M. Sheppard	10:VIII:1969	2	5	5	3		
B. Rotger	17:VIII:1969	28	27	28	11	1	3
N. L. Rumpp	20:VII:1970	6	12	11	10		
J. M. Sheppard	20:VII:1970	13	14	12	10		3
N. L. Rumpp	8:VIII:1971	1	6	1			
	Subtotals	51	67	57	34	1	7
Totals (217 specimens)		118		91		8	

COMPARISON WITH OTHER SUBSPECIES OF *C. WILLISTONI*.—All specimens of the type series are similar in marking and reasonably homogeneous in size, but their color varies. In the majority, the color is blue-green, similar to ssp. *pseudosenilis* and ssp. *praedicta* of the Death Valley Hydrographic System of California and Nevada, but unlike these, ssp. *sulfontis* has a few hairs between the eyes, but not nearly so many as are found on the more eastern subspecies *willistoni, hirtifrons* and *estancia*. A lesser number, making up nearly the balance of the population, is brown or bronze in color, similar to the eastern subspecies. The only known location for ssp. *sulfontis* is near Willcox where it is isolated by great distances from all other populations of *C. willistoni*. This isolation is especially significant because *C. willistoni* is usually not found in the Colorado River drainage system[1] as reported by Rumpp (1961: 168), although it has been located now in Arizona, a fact not known at that time. *Cicindela willistoni* shows a preference for lacustrine salt flats, although it may also invade marshy areas and semi-dry river beds where saline muds are exposed. Depending on elevation and temperature, it may emerge early in the year at lower elevations, much later at higher altitudes. In the Sulphur Springs Valley the climate is normally dry in May and June and remains that way until the start of the rainy season in mid-July, at which time ssp. *sulfontis* suddenly appears in numbers on the Willcox Playa where it remains in evidence throughout the rainy season. The larva builds a turret on the playa in the fashion of ssp. *hirtifrons* as reported by Willis (1967:176-177).

DISTRIBUTION OF *CICINDELA WILLISTONI*.—*Cicindela willistoni* has an extensive distribution in western United States. The species ranges throughout the Great Basin and that part of the Basin and Range province extending into southeastern Arizona, but nearly exclusive of the Colorado River drainage system. East of the Rocky Mountains it occurs in Wyoming, Kansas, Oklahoma, Texas, and New Mexico. It may be found wherever there are wet playas, defined as seasonal salt flats or perennial lake beds. The various subspecies from the eastern side of the distribution are a bright bronze color and bear a deeper middle band, usually with very broad to confluent maculation. In these the head always bears a number of long decumbent hairs (Willis, 1967: 303). They may be geographically distinguished as ssp. *willistoni* of Wyoming; ssp. *hirtifrons* of western Kansas, Oklahoma, Texas, and northeastern New Mexico; ssp. *estancia* the endemic population of the Estancia Valley in central New Mexico, and finally ssp. *funaroi* of Jemez Creek in northcentral New Mexico. In the Great Basin, most populations are of ssp. *echo*. These may be subdivided into the eastern or Bonneville *echo* populations, and the western or Lahontan *amadeensis* populations, with such little differences in habitus and color as to be considered synonymous (Cazier, 1936:157). The name *spaldingi* was proposed by T. L. Casey (1924:14) for one bright green, broadly maculated specimen from Calleo, Utah. This is in a region encompassing widely variable populations of ssp. *echo*. These populations were sampled by the author on 29 May 1970 at Blue Lakes, Tooele County, Utah, at the edge of the Great Salt Lake Desert, approximately 80 kilometers northwest of Calleo. Another location is at Fish Springs Wildlife Refuge, Juab County, Utah, also at the edge of the Great Salt Lake Desert and 25 kilometers east of Calleo. This last site was visited by the author on 4 May 1962, and by Lawton and Willis (1974:51) on 24 July 1971. These populations are extremely variable in that a few individuals are like Casey's *spaldingi*, while others resemble ssp. *estancia;* however, the great majority of specimens is typical of ssp. *echo*. The third largest hydrographic entity of the Great Basin is the Death Valley system where *C. willistoni* is interspersed with populations of ssp. *echo*, ssp. *pseudosenilis,* and ssp. *praedicta*. Here colors trend to green or dark blue-green, with or without maculation. In all of the Great Basin populations from Utah and Nevada, southern Idaho, and eastern parts of Oregon and California, the vertex bears only a few hairs or none at all.

Cicindela pulchra dorothea Rumpp, new subspecies.
(Figures 1b, 2.)

DESCRIPTION.—Large in size, form robust; head, prothorax and elytra brilliant metallic-cerise or wine-red. Elytra with definite maculation, sometimes fully connected along sides. HEAD: Brilliant red on vertex from eye to eye, fringed with gold and green before shading into the bright deep

[1]An exception exists in the Ft. Bridger, Wyoming population of ssp. *willistoni*. This area is connected hydrographically to the Green River, the main tributary of the Colorado River.

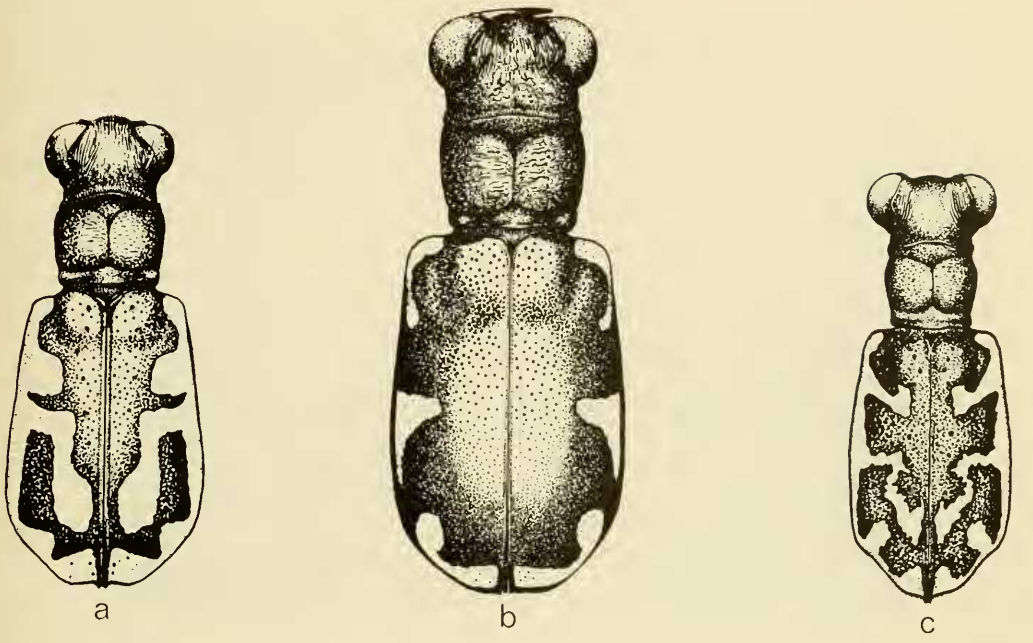

Figure 1. Dorsal views of: a. *Cicindela willistoni sullontis*; b. *C. pulchra dorothea*; and c. *C. nevadica citata*. Scale indicates 10 mm.

blue that covers the underside. Slightly rugose on the vertex, wrinkled near the eyes; deep setigerous punctures on the frons. Vertex with sparse erect white hairs, frons covered with long white decumbent hairs, genae bare. First four segments of the antennae bright green; first segment with over twenty stiff hairs on the outer edges, second segment bare, third and fourth with a sparse row of white hairs on the outer edges, with one setigerous puncture on the inner tips. Clypeus bright blue-green, with two setigerous punctures. Labrum white with a narrow dark edge, tridentate, with six setigerous punctures bearing long white hairs close to the outer edge. THORAX: Pronotum as broad as the head excluding the eyes, broader than long by a ratio of 4 to 3; broadest at the forward one third, then slightly tapering inward along a slight curve to the rounded basal angle. Surface finely rugose, brilliant red fringed with gold and green. Anterior and basal impressions deep, bright blue fore and aft respectively of these impressions; median impression very narrow, shallow, colored green. ELYTRA: Brilliant metallic red throughout, except for the very narrow outer edge which is blue with a row of green punctures. Surface punctured, these punctures deepest nearest the base, very shallow toward the apex. Suture golden-green. Maculation complete but reduced in extent; central band triangular, broadest at the edge of the elytra, very slightly recurved downward, reaching nearly half way to the suture; humeral lunule shallow at its tip, sometimes connected to the central band; apical lunule narrow, ending in a shallow dot, then narrowly connected to the middle band. UNDERSIDE: Bright deep blue. Proepisterna covered with long decumbent hairs; meso- and metaepisterna with shorter decumbent hairs. Upper abdominal segments with sparse white hairs on the sides, and long white hairs at the bottom edge of the 3rd, 4th, and 5th sternites; pro- and mesocoxae with long recumbent hairs, metacoxae bare; trochanters bare except for one setigerous puncture at the tip of those of the front and middle legs; femora blue with long hairs, more so on the anterior ones than on the middle and back ones; tibiae blue-green with rows of stiff white bristles, apical spurs about two thirds the length of the first tarsal joints; tarsal joints with several erect hairs, especially at tips; tarsal claws unpigmented, short, about half the length of the fifth tarsal joints. DIMENSIONS: Male - length 15.2 mm, width 6.0 mm. Female - length 15.6 mm,

Figure 2. Habitat of *Cicindela pulchra dorothea* south of Williston, Arizona on 26 July 1964. In the distance is a water filled pond.

width 6.4 mm.

ETYMOLOGY.—This insect is named in memory of my late wife, Dorothy, who collected many of the specimens in the initial large series.

THE TYPE SERIES.—There are 78 specimens in the type series. This includes the holotype male, the allotype female, and 44 topotypical paratypes collected by N. L. and D. H. Rumpp at the type location 5.2 to 6.2 kilometers southeast of Willcox, on 26 July 1964, and an additional specimen collected on 11 September 1965. Five paratopotypes were captured on 21 May 1970, three on 16 July 1974, twelve on 17 July 1974, and one more on 6 August 1975, all by the author. Two paratopotypes were collected by Dr. John Stamatov on 8 August 1971. The series also includes one paratype from 11.3 kilometers west of Douglas, Arizona, dated 6 August 1965.

Distribution of the type series: Holotype male, type no. 12529 in the California Academy of Sciences; allotype female, 66 paratopotypes and one paratype in the NLRC. Two paratopotypes deposited in each of the collections of the AMNH, the USNM and the CAS. Two are in the private collection of Dr. John Stamatov.

COMPARISON WITH *CICINDELA PULCHRA PULCHRA*.—From the time it was described by Thomas Say in 1823, *Cicindela pulchra* was considered a monotypic species from midwestern United States, ranging from Montana to Texas. Subspecies *pulchra* is larger, generally immaculate, with a color varying from dark red to deep violet. Some specimens, and these are few, have a triangular marginal middle spot not extended at the sides, sometimes with two dots representing a vestigial humeral lunule; otherwise the border of the elytra is broadly blue. Subspecies *dorothea* has a brighter red color, often with strong green reflections when viewed from an angle. In many specimens the white maculation is connected along the outer edge of the elytra, while in a few the maculation is reduced to dots. Less than ten percent of the specimens in the type series have a narrow middle band with blue connections along the outer edge of the elytra, and whereas these resemble the rarely maculated specimens of ssp. *pulchra*, the color is typical of ssp. *dorothea*, as is the smaller size.

Although ssp. *dorothea* is now isolated in southeastern Arizona, it was probably derived from the ancestral Rio Grande system during the Mio-Pliocene when the flow of the ancestral upper Colorado River drained east, and the Continental Divide was west of the valley, as will be discussed later. Now that this subspecies occupies a region that drains into the Yaqui River

system, it will probably be found in northern Sonora, especially since it has been located a few meters from the Mexican border west of Douglas, Arizona.

Some New Mexico specimens of C. *pulchra* from the USNM, AMNH, and private collections were examined. Those from the northwest or Farmington district can be identified with ssp. *pulchra,* whereas those from the southwest or Silver City district appear to identify with ssp. *dorothea,* as do those from the trans-Pecos region of western Texas.

Cicindela nevadica citata Rumpp, new subspecies
(Figure 1c.)

DESCRIPTION.—Medium size, body narrow, color brownish bronze with green micro pits, maculation of elytra narrowly connected along the outer edge. HEAD: Small relative to body size but with salient eyes; finely granulate vertex, frons very narrowly striate. Color green suffused with bronze. Pilosity of medium density on vertex, frons, and clypeus. First 4 joints of antennae green with bronze reflections on last 3 joints; first joint with 12 to 15 white recumbent hairs, 2nd joint bare, 3rd and 4th with 2 to 4 short hairs on outer edges and 2 setigerous punctures at tips. Clypeus white, barely produced in front, unidentate, ratio of width to length is 3 to 1; it bears 16 to 18 setigerous punctures located near anterior edge in two irregular rows. THORAX: Pronotum narrow, about as broad as the head excluding the eyes, cylindrical, length equal to width, finely rugulose, color greenish bronze. Anterior impressions of medium depth, basal impressions deeper, median impression shallow; sparse white decumbent hairs cover the top surface, more so at the edges, top, and bottom leaving the disc nearly bare. ELYTRA: Long, narrow, widest at the middle and twice as wide as the pronotum. Male - sinuous near tip, finely serrulate in this region; tips end in spines. Female - more sinuous and indented; terminal spines are smaller. Color brown except for center half from suture outward which is bronze; pitted throughout, pits green. A row of small green punctures descends near the suture, two rows of small punctures are located in the humeral impressions. The maculation is white and of typical *nevadica* design, except that the middle band is more narrow where it enters from the outer edge, and the central extension is longer; all markings are narrowly connected along the sides. UNDERSIDE: Mostly shiny brown with green reflections, however the genae are bright green, narrowly striate and covered with dense decumbent white hairs. The proepisterna are bronze with green reflections, densely covered with long white decumbent hairs; meso- and metaepisterna similarly clothed with long white hairs; pro- and mesocoxae also clothed with long white hairs, metacoxae bare; trochanters unpigmented, bare except for a setigerous puncture at tip of pro- and mesotrochanters. All abdominal sternites clothed with decumbent hairs on outer halves, with a few hairs at forward edges centrally. Fore and middle humeri with several rows of dense white hairs on the outer and inner sides; posterior humeri sparsely covered with non-overlapping hairs, none on outer sides. Tibiae bronze with greenish reflections, sparsely bristled. DIMENSIONS: Male - length 10.3 mm, width 4.2 mm. Female - length 11.0 mm, width 4.4 mm.

ETYMOLOGY.—The name *citata* alludes to the insect's fast running over moist sandy lacustrine shores.

THE TYPE SERIES.—The type series consists of 48 specimens. The holotype male was collected at the edge of the central playa 8 kilometers west-southwest of Willcox on 20 July 1970. The allotype female is from 2.9 kilometers south of Willcox, captured on 8 August 1955. Forty-six paratopotypes were collected near Willcox at sites such as Twin Lakes, nearby ponds, or at the northern edge of the Willcox Playa; all were collected from July through August between the years 1955 and 1975.

The holotype is deposited in the collection of the California Academy of Sciences as type no. 12,528. The allotype and 29 paratopotypes are in the NLRC. Paratopotypes in private collections are: Sheppard 3, Clifford 6, and Pearson 2. Two each were deposited in the AMNH, the USNM, and the CAS collections.

VARIABILITY: Most of the specimens in the type series are similar to the described type except for two specimens. One is a large female 12.4 mm long, with more cupreous coloration, the other a very small male only 9.1 mm long.

COMPARISON WITH OTHER SUBSPECIES OF *CICINDELA NEVADICA*.—The nominate subspecies *nevadica* of the Great Basin region of Nevada and California is of a coppery bronze with green reflections, somewhat similar in color to ssp. *citata*. The typical form of ssp. *nevadica* is reputed to be from Ash Meadows, Nye County, Nevada,

although LeConte (1875:159) merely reported it from Nevada. In the Nevada populations of ssp. *nevadica* the middle band seldom has any extension along the border, whereas in California populations there is usually a narrow extension along the border, sometimes connecting all the markings. The elytral pattern of the California populations more nearly matches the woodcut accompanying the description by LeConte, but he also states in the notes following his description that the markings were not connected along the margin. The markings of ssp. *nevadica*, where there is a connection along the outer border, differ from ssp. *citata* in that the middle band, where it enters from the edge, is broader in the former than in the latter; furthermore, the extension of this band is much deeper and narrower in ssp. *citata*. Subspecies *tubensis* differs from ssp. *citata* in that it has a red color, and although its maculation is always connected along the margin, these markings are much broader. Subspecies *knausi* of the upper Rio Grande basin is more nearly like ssp. *citata* in markings, but it also has slightly broader markings and less greenish coloration. Subspecies *citata* fits best between ssp. *nevadica* in color, and ssp. *knausi* in markings. The range of ssp. *citata* is the Sulphur Springs Valley, possibly into the Yaqui River system of Sonora. Those from the northern shores of the Gulf of California, specifically from Puerto Peñasco, can be identified with this subspecies.

ECOLOGICAL ASSOCIATIONS OF *CICINDELA* SPECIES OF THE SULPHUR SPRINGS VALLEY

There are seventeen species of the genus *Cicindela* in the Sulphur Springs Valley. These are separated below according to their ecological associations. Comparisons of related species and subspecies are given for some of the seventeen.

On wet flats, at the edge of water

1. *C. praetextata erronea*. This bright green or blue-green subspecies is endemic to the valley. It may be found on the northern shore of the Willcox Playa, and from the wind-formed ponds to Croton Springs. It is strikingly different in color from the bronze ssp. *praetextata* of the Colorado River drainage system, and from the red ssp. *fulgoris* of the Rio Grande system and upper regions of the Little Colorado River.

2. *C. marutha marutha*. When individuals of this subspecies emerge at the start of the summer rains, they form the largest populations along the mud flats of the ponds near Willcox. They will also invade marshy grasslands for they are not restricted to open areas, and at night they will come to light. This population is made up of nearly all pure grass-green individuals. Only 4 percent of the total are red. Most other populations of *C. marutha* in Arizona and New Mexico contain a high percentage of red individuals, but the northern ones contain the highest percentage of this color. In southeastern Utah there are pure red populations which should be referred to ssp. *rubicunda*.

3. *C. haemorrhagica*. The valley's population contains rather small, well marked individuals which have most often been identified with ssp. *woodgatei*. There is a resemblance to *C. carthagena carthagena*, especially in the median widening of the elytra and the angle so produced where the outer edges converge toward the tip. Individuals are found at the edge of water, usually on the darker spots where they segregate from other species.

4. *C. nevadica citata*. Individuals are relatively scarce in the valley, most being found immediately south of Willcox. This scarcity may be attributed to the high salinity of the local flats, because elsewhere this species seems to prefer damp sand, free from salt incrustations.

In grassy marshlands and very wet spots

5. *C. tenuisignata*. This is a brown monotypic species common to the Rio Grande system, the lower Colorado River drainage system, and Sonora. Individuals prefer damp as well as wet sandy soil.

6. *C. punctulata chihuahuae*. This is a grassland tiger beetle that is relatively rare in the valley. When found it will be in wet places. Individuals exhibit a variety of colors, from a bronzy green to a bright blue, with or without maculation. Bluish green is the most common color.

7. *C. nigrocoerulea nigrocoerulea*. This subspecies is polymorphic with individual members exhibiting a variety of colors that range from dull green to deep blue to black; blue-black is the predominant color. Individuals may be found most frequently in the thicker marshy areas and muddy spots, sometimes in great abundance.

8. *C. horni horni*. This is also a polymorphic subspecies with colors varying from metallic green or bright blue, to black. It is widely dis-

tributed in the valley from Douglas to Willcox, from the lowest grassy areas to upland meadows.

9. C. *sedecimpunctata sedecimpunctata*. This is a very common subspecies in southern Arizona, Sonora, and the Rio Grande system. It has a tolerance for high altitude, having been located in the Pinalino Mountains at elevations of 2700 meters, but always near ample water supplies. Although it is related to, and resembles C. *haemorrhagica*, individuals are noticeably smaller than in that species.

On muddy flats of the Willcox Playa

10. C. *willistoni sulfontis*. Members of this subspecies emerge in great numbers on the playa south-southwest of Willcox after the rains begin in mid-July and the surface of the playa becomes mucky. This form was first discovered at one of the ponds in the wind-built area south of Willcox, an area which it seldom invades. One individual was captured here following a long flight from the edge of a pond over a dry clay spot populated by C. *pimeriana*. Individuals are strong fliers, making frequent flights of as long as 10 meters, with very brief rests between flights.

On dry flats, not far from water

11. C. *pimeriana*. This monotypic species is the most common one found in early spring and again in autumn. Its characteristic color is brilliant metallic green, although the few spring individuals that survive until October become dull black. This tiger beetle is found only in the Sulphur Springs Valley and the San Bernardino Valley to the southeast. This last area contains the type locality at the San Bernardino Ranch (the old Slaughter Ranch) on the Mexican border. The species is related to C. *pulchra*, with which it shares a general area south of Willcox, but its preferred habitat is on bare clay banks near water. An individual's flight is long and singular, and it makes such flights between long rest periods, possibly as a defense against asilid robber flies that prey upon it. The fly's attack strategy is to swoop upon the beetle as the beetle takes to flight. The fly then embraces its prey with its legs while still flying and inserts its beak at the juncture of the open elytra, directly into the mesosternum, stunning the beetle almost immediately. The flight of the asilid is so slowed by this load that fly and prey can be netted with ease. Five captures were made with C. *pimeriana* as the fly's victim, and once with a C. *marutha* as victim.

12. C. *ocellata ocellata*. This small dark-brown subspecies belongs to the Sonoran fauna and is widely dispersed throughout southern Arizona. It differs most noticeably from ssp. *rectilatera* of the Chihuahuan fauna by its rufous abdomen.

In grasslands, away from water

13. C. *pulchra dorothea*. This strikingly beautiful tiger beetle is found exclusively on open flatlands covered with clumps of grass. The beetle emerges from these clumps to fly onto bare spots in one long flight. There it will either remain in the open where it will seek the shade of grass, or it will rapidly run into the nearest clump of grass and disappear from view.

14. C. *lemniscata lemniscata*. This small red tiger beetle with pale legs and longitudinal maculation seeks open spots far from water. When disturbed it quickly takes to wing, but it is a weak flier with an erratic flight. Although often seen in the daytime, its habits are more nocturnal than diurnal, and at night it will come to light in great numbers.

15. C. *debilis*. This small dull-green tiger beetle is related to C. *lemniscata*, but unlike that species it rarely flies. It prefers heavy grass where it seeks the densest parts for refuge. It is rarely encountered in the daytime and may be nocturnal in habit. The species will usually not fly, but when coaxed to do so its flight is erratic and very short, only a few decimeters in distance. The green C. *debilis segnis* was described as a variety from southern Arizona by Harris (1913:69), but Cazier (1954:287), after studying large samples from southern Arizona and Durango, Mexico did not favor retaining this subspecies. A population of darker individuals of this species was found near Willcox, and one with brighter green individuals was found near Douglas. However, these color variations may have been due to the age of the individuals sampled, the older possibly being the darker.

16. C. *obsoleta santaclarae*. This is the largest tiger beetle in the valley, often measuring 17 mm in length. It too is polymorphic for it may be green, blue, brown, black or red, although the predominant color seems to be green. The elytra are spotted, and a vestigial middle band is indicated by two dots on each elytron. The species is robust and its members are excellent fliers. Its flight is long, sometimes on the order of 100 meters, and often very high. It is found in grasslands on well-drained alluvial slopes, particularly

along the edges of the valley. In the grasslands west of Douglas it is encountered with *C. nigrocoerulea*, *C. pulchra*, *C. horni*, *C. lemniscata*, and *C. debilis*.

Tree areas near water

17. *C. viridisticta arizonensis*. This is another very small tiger beetle related to *C. debilis* and *C. lemniscata*. Near Douglas it is found among grasses on the slopes of drainage ditches in the chaparral-covered plains, while at Kansas Settlement it is found in grass near willows and tules that grow at the sides of irrigation canals. The species is a weak flier with a short and erratic flight. It prefers to remain on the ground where it will move with great speed and agility through the grass.

KEY TO THE SPECIES OF *CICINDELA* IN THE SULPHUR SPRINGS VALLEY

1a. Abdominal segments rufous 2
1b. Abdominal segments black, dark blue or greenish 4

2a. Elytra gradually widening to apical fourth; color brown 3
2b. Elytra widest at middle or basal third; color black ..... *haemorrhagica*

3a. Post, median, lateral and apical dots present ..... *sedecimpunctata*
3b. Post, median, lateral and apical dots absent ....*ocellata*

4a. Front trochanters only with seta (small species, less than 8 mm long) 5
4b. Front and middle trochanters with seta 6

5a. Elytra bright red, shiny, deeply punctate; markings consisting of a longitudinal line .....*lemniscata*
5b. Elytra dull grayish brown with a longitudinal row of green foveae; middle band and apical lunules present ..... *viridisticta*

6a. Small species, less than 9 mm long (velvety green in color, elytral maculation consisting of a wide partially submarginal border) ..... *debilis*
6b. Larger species, 10 mm long or longer 7

7a. Genae covered with decumbent hairs 8
7b. Genae bare 9

8a. Antennal scape with subapical sensory hairs only; bright green, occasionally red (elytra with feeble apical spine) .....*marutha*
8b. Antennal scape with decumbent hairs below the subapical setae; brown or bronze with greenish reflections ..... *nevadica*

9a. Frons or vertex to some extent pilose 10
9b. Frons and vertex bare except for ocular setae 12

10a. Pilosity of vertex sparse, frons bare; color dark green or brown; (maculation complete and joined at margin) ..... *willistoni*
10b. Pilosity of frons and vertex medium to dense; color brilliant 11

11a. Green or blue-green; immaculate or with very small apical dots, rarely any median dots ..... *pimeriana*
11b. Red; maculation marginal consisting of humeral, median, and apical spots, sometimes connected; (large in size) ..... *pulchra*

12a. Under surface sparsely to densely pilose laterally.....13
12b. Under surface bare except for a few scattered hairs, especially on sides of metasternum .....*horni*

13a. Proepisterna densely clothed with long white decumbent hairs; maculation complete ..... *praetextata*
13b. Proepisterna bare or sparsely clothed with hairs 14

14a. Elytra with subsutural row of blue foveae from base to apex 15
14b. Elytra with shallow or obscured foveae, or none at all 16

15a. Color green or blue-green; elytra narrow and slightly widening to apical fourth, microserrulate near apex; maculation consisting of small dots except for a narrow apical lunule ..... *punctulata*
15b. Color dull green, dark blue or blackish blue; form robust; elytra evenly arcuate, broadest at middle, not serrulate near apex; maculation usually absent ..... *nigrocoerulea*

16a. Elytra with shallow or obscured foveae; maculation narrow and complete, descending portion of middle band long; smaller in size ..... *tenuisignata*
16b. Elytra without foveae; maculation consisting of interrupted dots; very large in size ..... *obsoleta*

CLASSIFICATION OF THE SULPHUR SPRINGS VALLEY *CICINDELA*

By using the characters contained within the male genitalia in conjunction with a few external characters, Rivalier (1954) arrived at a natural classification of the genus *Cicindela*. Based partly on his system, the species of the Sulphur Springs Valley are tentatively classified below. Some collecting locations in the Sulphur Springs Valley are indicated in brackets for each species.

Subgenus *Cicindela*[2]

C. *pulchra* group
  C. *pimeriana* LeConte [Willcox, Douglas, Croton Springs]
  C. *pulchra dorothea* Rumpp [Willcox, Douglas]

C. *willistoni* group
  C. *willistoni sulfontis* Rumpp [Willcox]

C. *punctulata* group
  C. *tenuisignata* LeConte [Willcox]
  C. *punctulata chihuahuae* Bates [Willcox]

C. *ruliventris* group
  C. *haemorrhagica woodgatei* Casey [Willcox, Kansas Settlement]
  C. *sedecimpunctata sedecimpunctata* Klug [Willcox, Douglas]
  C. *ocellata ocellata* Klug [Willcox, Douglas]

[2]Includes all of Rivalier's (1954) *Cicindela* and *Cicindelidia*.

C. *obsoleta* group
C. *nigrocoerulea nigrocoerulea* LeConte [Willcox, Douglas, mountain slopes]
C. *obsoleta santaclarae* Bates [mountain slopes, Douglas]
C. *horni horni* Schaupp [Willcox, Elfrida, Douglas, mountain slopes]

Subgenus *Habroscelimorpha*

C. *circumpicta* group
C. *praetextata erronea Vaurie* [Willcox, Croton Springs]

Subgenus *Cylindera*[3]

C. *nevadica* group
C. *nevadica citata Rumpp* [Willcox]
C. *marutha marutha* Dow [Willcox, Croton Springs]

C. *lemniscata* group
C. *lemniscata lemniscata* LeConte [Willcox, Dos Cabezas, Douglas]

C. *celeripes* group
C. *viridisticta arizonensis Bates* [Willcox, Kansas Settlement, Douglas]
C. *debilis Bates* [Willcox, Douglas, mountain slopes]

DERIVATION OF THE *CICINDELA* IN THE SULPHUR SPRINGS VALLEY

GENERAL. —An underlying assumption made in this section is that tiger beetles of the arid regions of the Southwest were dispersed by way of hydrographic paths connecting various basins during wetter periods, or so-called pluvial times. These periods of higher rainfall were generated during glacial cycles when storm cyclones moved south ahead of advancing ice sheets in the north. Another assumption is that orogeny was also a force that had a direct impact on the direction of rivers and the distribution of rainfall. From the present distribution of the Cicindelidae in the Southwest, coupled with some data on past geomorphology, a number of speculative routes can be inferred.

EASTERN COLORADO–RIO GRANDE HYDROGRAPHIC CONNECTIONS. —Most of the species in the valley were derived from the Rio Grande–Chihuahuan fauna. To better understand this strong influence from the east, it is essential to realize that the Colorado River drainage basin of today did not always drain into the Gulf of California. There is much evidence indicating that during mid-Cenozoic (Miocene) the drainage patterns were to the east. The latest review of the evolution of the Colorado River explains this pattern. The following partial quotation is from McKee et al. (1967: 54):

> "General drainage patterns in northern Arizona during Stage 3 (mid-Cenozoic drainage patterns) — At least two different drainage pattern systems, separated by the Kaibab upwarp, are believed to be present. The eastern system, here called the ancestral upper Colorado system, in inferred to have flowed southward from Utah then southeastward across northeastern Arizona approximately along, or somewhat north of, the present Little Colorado River course, but in a reverse direction. . . . This drainage may possibly have connected with an ancestral Rio Grande drainage flowing to the Gulf of Mexico."

The distribution of *Cicindela* along the upper course of the Little Colorado River prompted the following statement by Rumpp (1961: 180): "The Little Colorado River was created during, and as a result of uplift. Prior to this, its upper basin was part of an eastern hydrographic system." This conclusion, although not as encompassing as that of McKee et al. is nevertheless similar. It was based on the occurrence of several species of *Cicindela* along the upper Little Colorado River, such as the large red *C. hirticollis* (ssp. *ponderosa*), and also *C. sperata*, *C. nigrocoerulea*, *C. fulgida* and *C. lepida*, all of which occur in the Rio Grande system. *C. fulgida* and *C. lepida* have spread as far as Utah. In the Rio Grande system *C. fulgida* displays a longer descending middle band, a characteristic that is also common to those populations of the upper Little Colorado River basin.

With the ancestral upper Colorado River draining eastward from mid-Miocene to some later undetermined time, it follows that the Continental Divide was farther to the west than it is today. This may have been the situation from Montana to southern Arizona. In this latter region the divide would have been west of the Sulphur Springs Valley such that the regional drainage would have been eastward eventually reaching the Gulf of Mexico, possibly as a port of the ancestral Rio Grande River system. Along such a hydrographic pathway, all of the middle Rio Grande species now found in southern Arizona could have migrated westward. These include *C. pulchra*, *C. tenuisignata*, *C. punctulata*, *C. nigrocoerulea*, *C. horni*, *C. obsoleta*, *C. marutha*, *C. willistoni*, *C. sedecimpunctata*, *C. ocellata*, *C. nevadica*, *C. lemniscata*. and *C. praetextata*. One species, *C. haemorrhagica*, is of a more Sonoran type which may have migrated eastward at that time. During this early migration period the species probably met few new conditions, but many environmental changes came in time. Because of varying ecologies the species adapted differently. Some subspeciated along the length of the migratory path, while others did so only at

[3]Includes all members of the subgenus *Ellipsoptera* Dokhtourow.

the extremes of the range. For example, *C. pulchra dorothea* subspeciated along the whole length of its southwestern expansion. Now that its range has been disrupted it remains as the same subspecies in the Sulphur Springs Valley, southern New Mexico (Silver City region), and trans-Pecos Texas (Alpine–Marfa region). The same holds for *C. nigrocoerulea*, *C. horni*, *C. sedecimpunctata*, and *C. punctulata*. Others that subspeciated only at the ends of this long route are *C. ocellata*, *C. obsoleta*, *C. lemniscata*, and *C. praetextata*. The *C. ocellata* representative of the middle Rio Grande River region is ssp. *rectilatera*, while in the same region *C. obsoleta* is represented by ssp. *vulturina*, both significantly different from their western counterparts. *Cicindela lemniscata* also has subspecies in the eastern and in the western parts of the range, both subspecies having extended their ranges sufficiently to have created a hybrid zone along the middle Rio Grande River region. *Cicindela praetextata fulgoris* is usually red but sometimes greenish with broad markings, while the common western ssp. *praetextata* is brown or bronze with narrower markings. The isolation of ssp. *erronea* next to a saline lake bed was described by Rumpp (1957: 149) as an exceptional case for *C. praetextata;* this isolation possibly explains the startling contrast in color between this bright green subspecies and the other subspecies. *Cicindela tenuisignata* is the only species that appears not to have diverged locally, retaining its monotypic form throughout its extensive range.

WESTERN COLORADO RIVER CONNECTIONS. —When the upper Colorado River flowed east (middle to late Miocene and possibly well into the Pliocene) there were normal north-south mountains in the region now occupied by the Grand Canyon and southwestern Utah. The Hurricane Fault marks the location of one such mountain range. This is specifically mentioned here because it is along this ancient fault that the large apterous and nocturnal tiger beetle *Amblycheila schwarzi* can be found, one population at the southern end of the fault at Peach Springs, Arizona (type locality), the other at the northern end in Diamond Valley, some 20 kilometers north of St. George, Utah. Between these populations flows the Colorado River through the impassable Grand Canyon. It is clear that at one time the river was not there, so the population was once continuous. If a river existed there in that period, it flowed westward. Neither did the Gulf of California exist at that time because the Lower California peninsular plate had not yet begun its movement outward and northward (movement did not occur until Pliocene time, about four million years ago). There is strong evidence that there was an outlet from this region to the Pacific Ocean during the Miocene and possibly later. At that time it is probable that the Continental Divide precluded the Rio Grande tiger beetles from reaching that region. But in time the Lower California plate, by its northward pressure, cut off drainage to the Pacific Ocean by raising the Tehachapi Mountains at the southern end of the Sierra Nevada range, thereby creating a region of internal drainage. A lake region developed during glacial times, eventually ending wholly or in part when the Colorado River cut through the Grand Canyon and supplied enough water to create a discharge to the Gulf of California. Trapped populations, originally derived from the Rio Grande basin could now expand westward wherever conditions would permit. Conversely, some western species could now migrate eastward into the expanding lower Colorado River basin.

Westwardly expanding species include *C. praetextata praetextata*, which in time reached the Virgin River Valley as did *C. punctulata chihuahuae*, this latter having been reported also with *C. tenuisignata* at Ash Meadow in the Amargosa Desert of Nevada by W. Knaus (1922: 194). Whether *C. nevadica* and *C. willistoni* ever made contact in this manner with their counterparts in the Sulphur Springs Valley is unknown; but at some time it could have happened, and that possibility cannot be discounted.

YAQUI RIVER HYDROGRAPHIC CONNECTIONS. —There are two typically Sonoran species in the valley. These are *C. debilis and C. viridisticta arizonensis*. They are not differentiated from their Mexican counterparts. Hubbs and Miller (1958: 115) found no evidence connecting Lake Cochise to the Yaqui River in pluvial times so that the present connection of the southern third of the valley to the Yaqui River must be of recent origin. This leads to the conclusion that these two species are recent intruders.

SPECIFIC ENDEMISM. —The only endemic species in the Sulphur Springs Valley is *C. pimeriana*, a member of the *'pulchra' group*, and a relative of *C. fulgida* from which it differs in color, lack of maculation, sparser pilosity, and a labrum which is less produced in front. These differences might be viewed as minor but for the fact

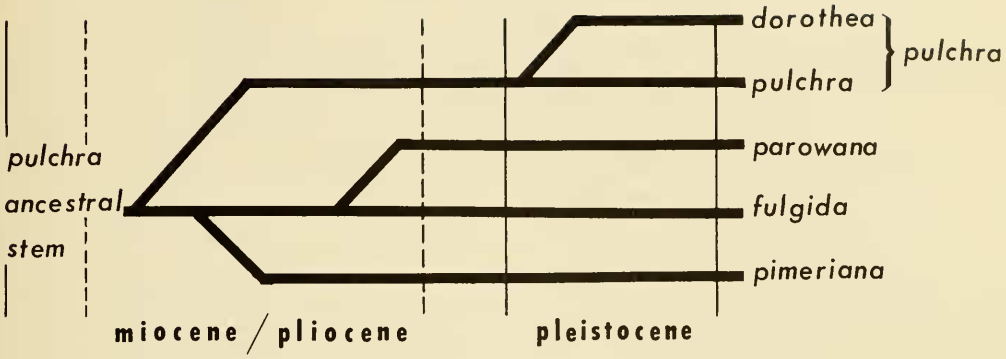

Figure 3. Hypothetical chronology of the four species in the C. *pulchra* group of the subgenus *Cicindela*.

that the male genitalia, while remarkably similar, have constant specific differences. How and when C. *pimeriana* came to be in this area is unknown. It could have arrived from the north or from the east as an offshoot of C. *fulgida*. Its relationship with other species of the *'pulchra'* group is of ancient origin, one that may be hypothesized as shown in Fig. 3.

Some species of the Sonoran *Cicindela* fauna are so isolated and distinct as to suggest the possibility that a region in southern Arizona and northern Sonora contained a specialized fauna since earliest Cenozoic times. These distinctive species are now reduced to relatively small areas, such as C. *pimeriana* in the San Bernardino and Sulphur Springs valleys, and C. *beneshi* and C. *rockefelleri* from the Gulf of California coast near Puerto Peñasco. Though isolated and distinct, all three have related species within close range.

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